

Research Article

# Adaptive patterns of anti-predator escape behavior in a globally introduced bird species

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## Abstract

Introduced species can represent quasi-experimental, anthropogenic case studies of both ecological and evolutionary principles. When these species are firmly established, competitive interactions between native and introduced species, including foraging, spacing, and breeding competition, may be among the ecological costs incurred from such species invasions. In turn, genetic and/or plasticity-driven changes in behavior and morphology could also take place in the invading species with increasing introduction lag (time since the onset of introduction). Critically, however, introduction lag is difficult to study in any single non-native population without long-term observations, and, instead, it requires geographically repeated measures of the focal response variables across invasive populations that were introduced at different times. Here we tested *a priori* predictors of predator-avoidance behaviors through the flight initiation distance (FID) assay of a widely distributed invasive bird species, the common myna *Acridotheres tristis*. The species was extensively and consistently sampled throughout most of its independently introduced ranges across all hemispheres. Critically, FID increased with greater introduction lag. We also detected additional functional patterns in that FID increased towards the rural range within a continuous metric of urban-rural gradient and also at shorter distances from the Equator. Any robust study of FID must also include proximate predictors as well and, accordingly, we found that FID increased with greater starting distance, with lower immediate human density, with flighted over walking escape responses, and at lower heights of a bird's perch above ground but was unrelated to myna group size. Respectively, these factors are informative about the sensory cues triggering anti-predator behaviors in invasive mynas and imply an adaptive set of patterns of anti-predator responses in the introduced ranges of this species. Control measures of invasive common myna populations should take into account their extensive behavioral and cognitive flexibilities and adjust the planned management methods accordingly.



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**Key words:** Anti-predator behavior, Indian mynahs, invasion latency, plasticity

## Introduction

Introduced species represent one of the major anthropogenically mediated global-change factors that threaten and reduce native biodiversity (Downs and Hart 2020). Accidental or deliberate species introductions can function as both ecological and evolutionary case studies (or “natural experiments”: Diamond and Robinson 2011) to understand the role of physical and biotic factors on potential species

establishment and spread, while also allowing for the documentation and analysis of evolutionarily novel interspecific interactions (Blackburn et al. 2009). When the same species has been introduced repeatedly at distant sites (i.e., metareplication), it can present a quasi-experimental system where biologically independent events can be analyzed within powerful statistical frameworks (Blackburn et al. 2009; Samas et al. 2013; Grim and Stokke 2016; Downs and Hart 2020; Magory Cohen et al. 2020). Specifically, the impact of introduction lag (i.e., time since the onset of introduction) on foraging, anti-predator, social and breeding traits is best studied across different populations, introduced independently at various times from the native ranges. Here we focus on such a study species and system, the common myna (*Acridotheres tristis*, hereafter: myna; Fig. 1), a successful global avian invader (Magory Cohen et al. 2019).

Understanding how an invasive species adjusts to the novel environmental conditions, and especially whether invasion success is enhanced in a world with globally increasing urbanized habitats (e.g., Moller et al. 2015; Sol et al. 2017), can shed light not only on the dynamics of the invasion process but also on the direction of the phenotypic changes, for example in morphological or behavioral traits. Such information on individuals from different populations can guide local conservation measures and inform more efficient control steps and effective management tools (Mikula et al. 2023).

Prior work on mynas has identified both morphological shifts along urbanization gradients within their introduced ranges (e.g., Old et al. 2014; Magory Cohen et al. 2021) and a more complex suite of cognitive traits that were prevalent at invasion fronts relative to core invasion areas or within the native ranges (Magory Cohen et al. 2020). However, the adaptive value of these morphological and cognitive traits was only hypothesized, and not tested, in ecologically-relevant functional contexts. Therefore, here we used a long-standing anti-predator response field-ecology paradigm, the Flight Initiation Distance (FID) assay (where an observer human represents a potential predator; e.g., Samia et al. 2017), to examine common mynas across much of their invasive global distribution to identify predictors of escape behavior at both the proximate and ultimate levels of analysis. The FID paradigm for birds has been developed and used extensively successfully for diverse tests of ecological (e.g., Diaz et al. 2021) and conservation concepts (e.g., Mikula et al. 2023).

If mynas behave so as not to treat some evolutionarily novel heterospecifics as potential predators (e.g., because unexperienced mynas have not yet evolved to recognize them specifically, i.e. evolutionary lag), then we predict that, functionally, we can detect lower FIDs at sites with shorter introduction lags. Indeed, in a prior study, mynas at recently invaded areas showed less neophobia compared to both sites with longer invasion histories and within their native ranges (Magory Cohen et al. 2020). In turn, we expected FIDs to be greater at sites with more diverse actual predatory species communities due to more risk, including tropical areas closer to the Equator (Martin 2015), at lower elevations (Díaz et al. 2013; Roslin et al. 2017; but see Sandercock et al. 2005; Andrade and Blumstein 2020), and at less urbanized areas (McCabe et al. 2018).

Additionally, we tested several proximate factors, including starting distance, height of perch above ground, myna group size, immediate human density, and the escape modality (running vs. flying away) as sensory predictors of FID (sensu Diaz and Moller 2023). We hypothesized that height and flighted escape re-



**Figure 1.** The common myna represents a successfully urbanized species in its native range (a Malaysia) and its flexible ecology allows it to successfully colonize even rural areas on isolated oceanic islands where it was released by humans (b Tahiti). Invasive animal species often share similar, especially urban, habitats (c New Zealand; in this case with introduced House Sparrows, *Passer domesticus*) and are often found in invasive vegetation (d Madagascar; in this case non-native pines *Pinus* sp.). Common mynas can reach very high local densities (e Madagascar; a small section of an 800-strong roosting flock), also due to their ability to use novel, anthropogenic food sources (f Israel). Photo credits: T. Grim.

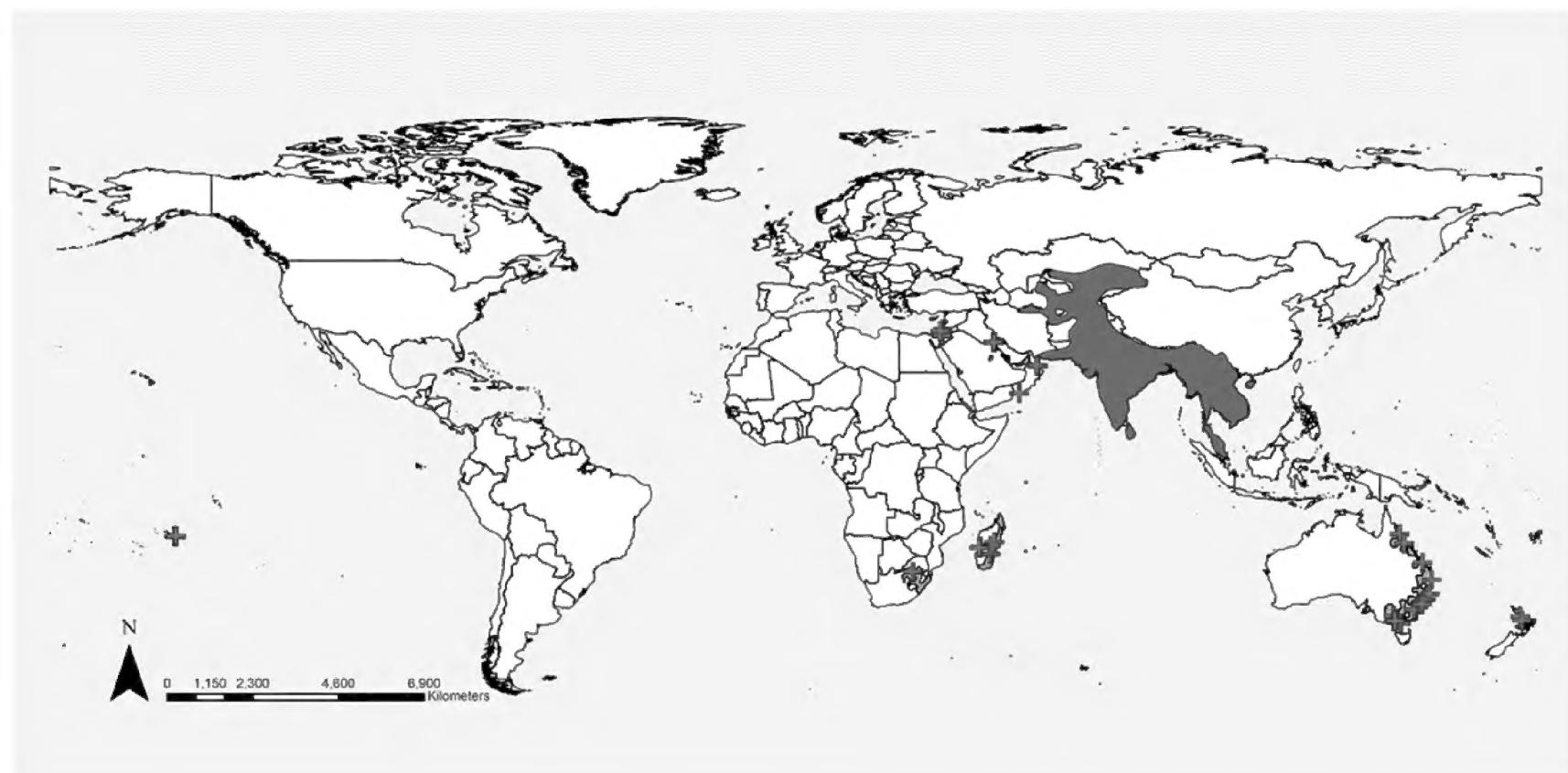
sponses will be negatively associated with FID, despite the complexity of these escape modalities (see Cooper and Blumstein 2015), whereas starting distance, myna group (flock) size, and immediate human density will be positively associated with FID (following Blumstein 2003; Samia et al. 2017; Morelli et al. 2019; Diaz and Moller 2023). This is because greater height would assure greater safety

from a ground-approaching (human) predator, larger conspecific groups would show greater vigilance (i.e., allow for faster danger detection), and taking flight assures a more rapid escape than walking away (Morelli et al. 2019; Diaz and Moller 2023). Further, a subject would be able to identify a potential predator at a greater distance when the latter begins its direct approach further away (i.e., at a longer starting distance). Finally, more humans in the proximity of the focal subject would represent a greater perceived predation pressure.

## Methods

Common mynas are native to South Asia, have been introduced to novel sites on five continents, including on several Pacific Island archipelagos, either as accidental releases of captive birds or deliberately imported agricultural control agents (Downs and Hart 2020). With arrivals and detections in non-native localities ranging from the early 19<sup>th</sup> century to present day (e.g., Magory Cohen et al. 2019; Beesley et al. 2023), the common myna is both a highly successful and locally rapidly spreading species, which often competes with native avifauna for valuable cavity-nests and food (the multiple negative effects of myna invasions are reviewed in Downs and Hart 2020; but see Lowe et al. 2011). Among hundreds of species of successfully established avian invaders it was even selected, with only two other species of birds, on the list “100 of the World’s Worst Invasive Alien Species” by IUCN (Lowe et al. 2000).

FID data on common mynas were collected consistently by a single observer (TG), thus avoiding any potential inter-observer bias. A total of  $n=451$  FID data points were collected across much of the invasive ranges of the mynas (Fig. 2), including 3 continents, 8 countries, 37 settlements, and 57 separate localities. FIDs were measured following established methods (e.g., Blumstein 2006; Moller 2008; Samia et al. 2017). Specifically, when an individual bird was located, the observer moved at a normal walking speed directly toward the focal subject.



**Figure 2.** Sampling locations (red crosses) for FID data outside the native (blue regions) and within the introduced (yellow regions; note that yellow color areas denoting Kuwait and Tahiti are too small and overlaid by red crosses marking sampling sites) ranges of common mynas. The distribution map was modified from Magory Cohen et al. (2021).

The starting distance was estimated between the point where the same sole observer (TG) located the bird (and started his approach towards it) and the bird's own original location. Flight initiation distance (FID) was defined as the distance between the approaching observer and the focal bird at the moment when it began to flee by either running away or taking flight. The distances were estimated by measuring first and assuming later that the observer's steps represented 1 meter distances. For each response data point of FID the following data were initially collected (in 2013,  $n=58$ ), its height, the locality's latitude and longitude (Fig. 2), its altitude above sea level (m), the city and country of the location, date, and time of day (hour), the starting distance, and the escape mode of the focal bird: whether on foot (running away) or by flight (flying away). In the later years of data collection (2017 onwards,  $n=394$ ), two additional variables were also collected: an immediate human density (the number of humans present within 50 m from the focal bird) and the flock size of conspecifics around the focal individual within 10 m (following Morelli et al. 2019).

Most specific locations included in the present study were visited only once, thus preventing any potential pseudoreplication (repeated sampling of the same individuals). In a few cases the observer did not manage to sample the whole locality (park, botanic garden, etc.) during one visit or to reach reasonable sample size; in such cases another visit was done but a different part of the same locality was checked. We accounted for these patterns statistically (see below).

To assign a quantitative score of each locality's urban-rural gradient at our study sites, we followed the urbanization assessment methodology of Seress et al. (2014). Briefly, this method used the 'UrbanizationScore' image-analysis software and quantified the degree of urbanization in  $1 \text{ km} \times 1 \text{ km}$  areas around a focal point based on Google Maps satellite images. Each rectangle area was divided to  $100 \text{ m} \times 100 \text{ m}$  cells (as is typical in ecological studies of urban-rural gradients on small birds, e.g., Bokony et al. 2012; Rodewald et al. 2013; Salmon et al. 2018), and in each cell, the software evaluated major land-cover characteristics: the proportion of buildings, vegetation (including brownfields, desert or beach sand, and arable areas), and paved surfaces (roads, parking allotments, etc.). Then, using the data on these land-cover features, we conducted a principal component analysis (PCA) to generate an 'urbanization score' variable (PC1) for each study site: this is a continuous variable suitable for standard statistical analyses, in which positive values represent the less urban (more rural) while negative values represent the more urban areas.

Finally, to assign year of introduction to each locality, we sourced city or regional-level data from Long (1981) for Australia, Madagascar, New Zealand, South Africa, Blanvillain et al. (2003) and Lever (1987) for French Polynesia, Hone (1978) also for Australia, Magory Cohen and Dor (2019) for Israel, Maniyar (2018) for Oman, and the Invasive Species Specialist Group (2011) for Kuwait. Because our research took place over a full decade, we calculated this "Introduction Lag" metric as the year when the FID data were collected minus the year of known or estimated introduction.

## Statistical analyses

We first generated two sets of standard least square mixed models, with restricted maximum likelihood (REML method), to assess first, 1A) the impact of all proximate predictors that we have collected upon the FID in mynas, using FID as the

response metric and starting distance, height, and escape mode as predictors, with location identity (locality and place combined: column “loc\_ID” in our data set available online at Figshare.com; see below) included as a random effect, for all data points collected across the study. Second, we analyzed a reduced sample-size model from the more recent years’ data points only to assess the impact of 1B) both all the previous and the additional proximate predictors upon FID in mynas, using FID as the response metric and starting distance, group (flock) size, height, immediate human density, and escape mode as predictors, with location identity (locality and place combined: column “loc\_ID” in our data set which is available online at Figshare.com; see below) included as a random effect. Finally, we generated a model to assess the impact of 2) all functional predictors collected upon FID in mynas, using starting distance, altitude, absolute latitude (to account for the distance from the Equator for both northern and southern hemisphere locations), urbanization score and introduction lag as predictors, and country included as a random effect. In order to fully account for all measured parameters, only saturated (i.e., full) models incorporating all fixed effects were constructed for hypothesis testing and effect estimation. No model selection techniques were employed that could potentially exclude relevant explanatory variables. This was also an appropriate approach because none of the predictors within each model were strongly correlated with each other (all pairwise  $|r| < 0.2$ ).

We included starting distance in both model types because it is the single best predictor of FID in prior studies (e.g., Mikula et al. 2023 and references therein), and also here (see below) and, thus, it always needs to be accounted for statistically in all models. In turn, the random effects for 1) vs. 2) were also different because each locality and place within the same region had the same year of introduction and, thus, we could not use “loc\_ID” as the random effect in this second type of model. Parameter estimates are presented with their associated standard errors (SE).

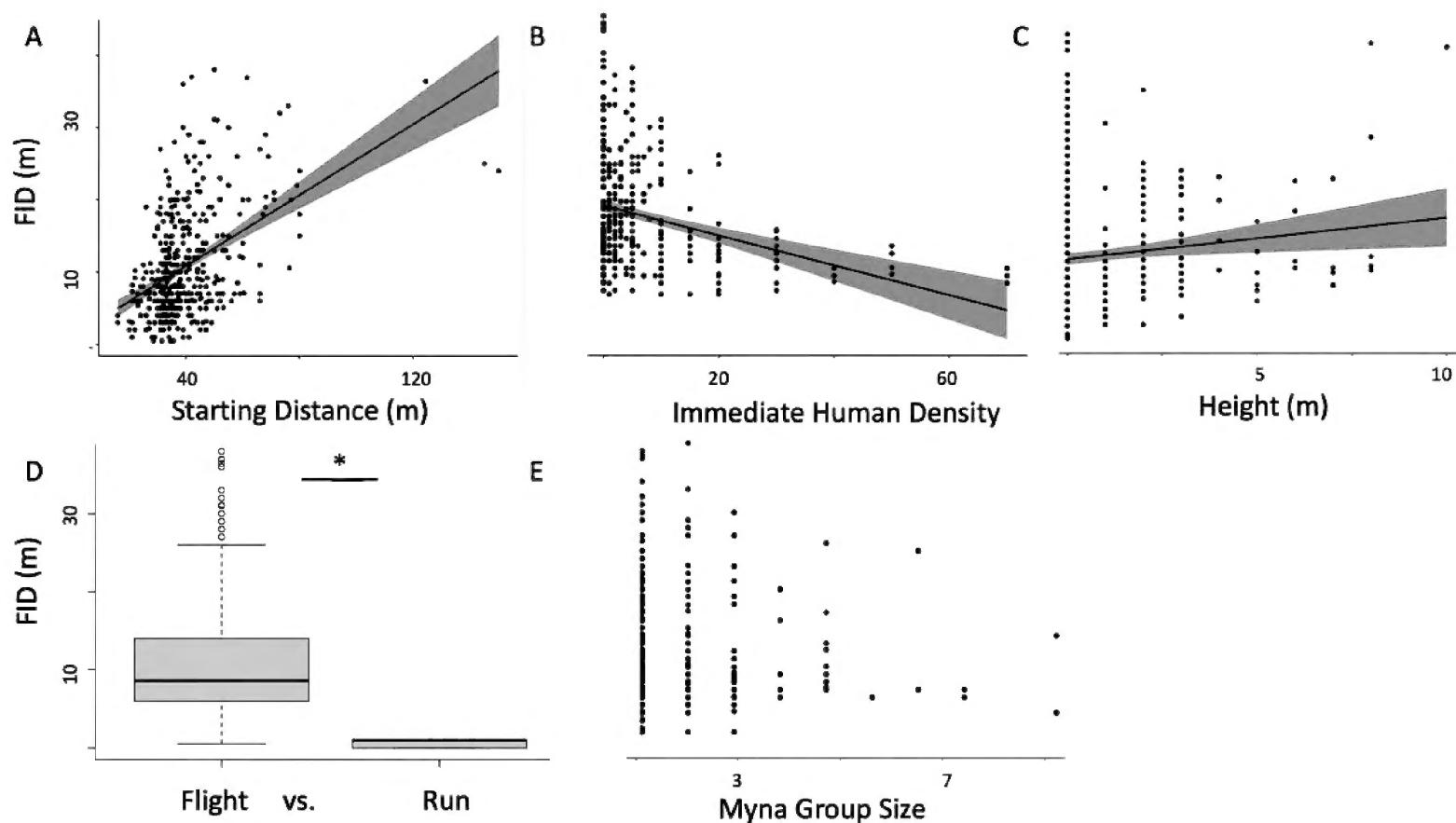
We did not log-transform the FID data in either model because doing so did not improve the  $W$  statistics of the Shapiro-Wilks test and so we also plotted the raw data in our figures. We used JMP 12.0 (SAS, Cary, NC, USA) for all statistical analyses and set alpha  $< 0.05$ . The data are made available through the following link: <https://figshare.com/s/485def8f8e1b851e8539>.

## Results

### Proximate factors

For the full data set (1A), we found that variation in FID was statistically significantly explained by all three predictors of our proximate factor model ( $R^2 = 0.80$ ): FID increased with greater starting distance, decreased at lower focal subject heights, and was greater when the myna escaped by flight (Table 1).

For the more recent data set (1B), we found that variation in FID was again statistically significantly explained by most of the predictors of our proximate factor model ( $R^2 = 0.80$ ): FID increased with greater starting distance (Fig. 3A), decreased both with immediate human density (Fig. 3B) and at lower focal subject heights (Fig. 3C), was greater when the myna escaped by flight (Fig. 3D), and did not co-vary with myna group size (Fig. 3E, Table 2).



**Figure 3.** Relationships between Flight Initiation Distance (FID, in meters) and proximate predictors. These include **A** starting distance **B** immediate human density **C** height **D** escape mode, and **E** group size. Raw data are plotted in all figures, instead of the model predicted leverages. When fitted in a full mixed model, starting distance, urbanization, absolute latitude and introduction lag (the last three predictors shown in Fig. 3) were significantly associated with FID while altitude was not. Shaded areas represent 95% CIs of the significant slopes; \* represents a significant difference.

**Table 1.** Statistical outputs of the full proximate factor models' impact on myna Flight Initiation Distance (FID).

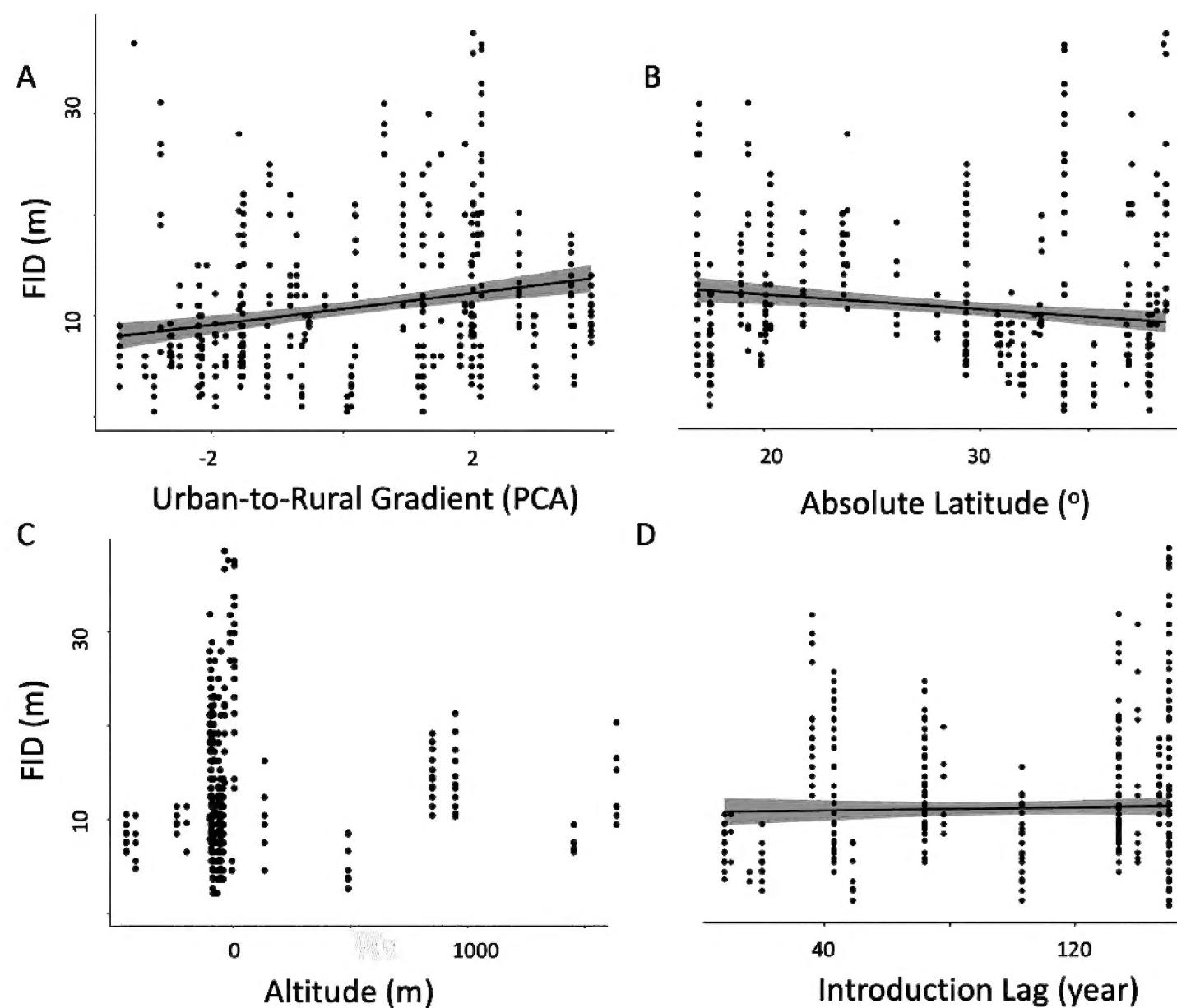
Predictor	Estimate	Standard Error	F-statistics	P-value
Starting Distance	0.13	0.01	$F_{1,405} = 77.0$	$P < 0.0001$
Focal Subject Height	-0.38	0.12	$F_{1,407} = 9.84$	$P = 0.0018$
Escape Modality	-0.83	0.22	$F_{1,407} = 14.06$	$P = 0.0002$

**Table 2.** Statistical outputs of the more recent years' proximate factor models' impact on myna Flight Initiation Distance (FID).

Predictor	Estimate	Standard Error	F-statistics	P-value
Starting Distance	0.13	0.02	$F_{1,355} = 65.02$	$P < 0.0001$
Immediate Human Density	-0.09	0.03	$F_{1,388} = 9.07$	$P = 0.0028$
Focal Subject Height	-0.40	0.13	$F_{1,354} = 9.82$	$P = 0.0019$
Escape Modality	-0.70	0.25	$F_{1,354} = 8.13$	$P = 0.0046$
Myna Group Size	-0.08	0.17	$F_{1,350} = 0.22$	$P = 0.6380$

## Functional factors

We found that FID was significantly explained by most of the predictors of our functional factor model ( $R^2 = 0.29$ ): FID increased with introduction lag (Fig. 4D), decreased with greater distance from the Equator (Fig. 4B), did not co-vary with altitude (Fig. 4C), decreased with greater urbanization (Fig. 4A), and increased with greater starting distance (Fig. 3A, Table 3).



**Figure 4.** Relationships between Flight Initiation Distance (FID, in meters) and functional predictors. These include **A** urban-rural gradient **B** absolute latitude **C** altitude, and **D** introduction lag. Raw data are plotted in all figures, instead of the model predicted leverages. When fitted in a full mixed model, starting distance (shown in Fig. 4A), introduction lag (years ago from 2023), absolute latitude, and urbanization were significantly associated with FID, while altitude above sea level was not. Shaded areas represent 95% CIs of the significant slopes.

**Table 3.** Statistical outputs of the more recent years' proximate factor models' impact on myna Flight Initiation Distance (FID).

Predictor	Estimate	Standard Error	F-statistics	P-value
Introduction Lag	0.03	0.01	$F_{1,157} = 5.24$	$P = 0.0234$
Distance from Equator	-0.20	0.05	$F_{1,386} = 14.70$	$P < 0.0001$
Altitude	-0.002	0.001	$F_{1,183} = 2.45$	$P = 0.1190$
Urbanization	0.92	0.16	$F_{1,433} = 32.62$	$P < 0.0001$
Starting Distance	0.22	0.02	$F_{1,444} = 114.56$	$P < 0.0001$

## Discussion

With a multi-continent distribution of its native and introduced ranges, both long-term and short recency of repeated establishment, and high levels of aggression and competitive success over other cavity nesting birds, the common myna represents one of the most successful and globally impactful avian invaders (Lowe et al. 2000; Downs and Hart 2020). Whether and how these repeated introductions may have led to local differences in morphology, cognition, and behavior have been the subjects of several recent studies on mynas both in their native and introduced ranges (e.g., Magory Cohen et al. 2020, 2022).

Yet, an ecologically validated assessment of locally adaptive diversity in myna phenotypes has been still missing across the species' diverse introduced ranges; we

aimed to fill this knowledge gap using the flight initiation distance (FID) assay as a well-established anti-predatory ecological paradigm (see Introduction). We found that, at the functional level, introduction lag was moderately but positively associated with FID, implying more tolerance of human disturbance and perceived predation in the more recent invasions. However, introduction lag was moderated by both distance from the Equator, with positive impacts on FID only within the tropics and negative impacts on it in the temperate zones. In turn, FID increased with introduction lag in rural areas and decreased in urban areas. These interactions are consistent with a differential impact of local predation pressure as a function of local establishment latency in an invasive prey species (e.g., Cooper et al. 2014). We detected greater FIDs in sites with greater predicted predation pressure on mynas (i.e., closer to the Equator and in less urbanized areas), though there was no effect of altitude in our data set.

These functional patterns parallel previous findings, namely that at the forefront of invasions (compared to core invasion areas and native ranges), mynas show behavioral syndrome traits that include less neophobia and more exploration in their foraging behaviors (Magory Cohen et al. 2020). The patterns also suggest that, in their introduced ranges, mynas show adaptive shifts in positively correlated anti-predatory and neophobic personality traits with greater introduction lag. It remains unclear whether these changes are driven by experience-driven plasticity, parental effects (including epigenetic patterns), and/or genetic changes effecting prosocial behaviors in mynas (Old et al. 2014; Magory Cohen et al. 2021; Beesley et al. 2023). When combining both of our functional and proximate (see below) predictors in a single model, we found that the statistical patterns with respect to predation pressure (proxies: distance from the Equator and urban-rural gradient) and introduction lag all remained significant predictors of FID, implying a general role of these ultimate factors in influencing predator-escape responses of common mynas.

Proximate cues for the common myna's FID responses may represent sufficient sensory information that is available for this medium sized avian prey species to make decisions about escape responses from potential predators, represented by approaching humans in the FID assay. Our findings support this sensory hypothesis, in that several proximate factors directly predicted the FID in this data set: specifically, the further the observer started to directly approach the myna(s), the earlier the subject(s) responded to the threat (leading to a greater FID) (see also Blumstein 2003). Similarly, the higher above ground a subject was positioned before the onset of the approach, the earlier (greater FID) it escaped.

In contrast, two of our proximate factors were related to FID in the opposite way from what we had predicted. With increasing immediate human density, FID was smaller, rather than greater (see Morelli et al. 2019), perhaps representing a confusion effect of being generally non-threatened by larger aggregations of humans but being less able to pinpoint the observer who is directly approaching the subject within that crowd. Alternatively, walking- or standing-by humans (as opposed to a directly approaching one) may be habituated to and, thus, not considered direct predators by mynas, and simply represent a positive correlate of living in more urbanized and less-predator prone sites (which is negatively correlated with FID in our data set; see above).

Similarly, we predicted that smaller FID would be associated with flying away escape responses (rather than running away responses), but we found the opposite to hold in our data set. This might be related to individual mynas' behavioral

syndrome: perhaps more easily flushed individuals are also more likely to escape on wing. We lack repeated observations of the same, marked individuals, thus we cannot assess other aspects of myna personalities, such as the repeatability of the escape style and FID consistency within the same individual. These topics deserve more research attention in the future. Finally, we detected no effect of myna group size on FID responses (similar to Morelli et al. 2022 but unlike Morelli et al. 2019), however the 95% CI of these data included only group sizes of 1 or 2, representing minimal variation in the predictor variable's data range. This is likely due to the territorial and monogamous pair bonded nature of the myna's social organization (Siddique et al. 1993) and also because larger flocks (like the roosting flock shown in Fig. 1E) were not flushed for this study.

Our findings demonstrate the flexibility of the common myna to adjust its behavioral responses to novel environmental conditions, including near-human habitats in an increasingly urbanized world. Smaller FID measured at sites of more recent invasions, of greater urbanization, more proximity to humans, may represent rapid habituation to people's presence. This may also have implications for conservation control measures of the invasive populations. Specifically, myna management schemes and methods selection should take into account this behavioral flexibility, (e.g., the decrease in boldness with invasion time), and adjust the methods accordingly in less urbanized areas and in areas with longer invasions to achieve a more efficient outcome (see also González-Lagos et al. 2021).

Overall, our globally extensive and methodologically consistent study represents an opportunity to step beyond the multifold independent introduction history of a globally invasive species. Spatially isolated non-native populations allow independent tests of ecologically-relevant adaptive scenarios about behavioral tactics and strategies that would be often hard or impossible to test in native populations only (e.g., Letnic and Dworjanyn 2011; Samas et al. 2014; Grim and Stokke 2016; Manna et al. 2017; Ruland and Jeschke 2020; González-Lagos et al. 2021).

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

Data were collected only on public land and the methods of the study were approved by IACUC Protocol #17259 at the University of Illinois, Urbana-Champaign.

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## Author contributions

TG: Conceptualization; Funding acquisition; Data collection; Writing – editing. RD: Conceptualization; Funding acquisition; Data curation and presentation; Writing – editing. MEH: Conceptualization; Funding acquisition; Data curation, analyses and presentation; Writing – first and subsequent drafts.

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## Data availability

Data are made available to the public through Figshare.com at the following link: <https://figshare.com/s/485def8f8e1b851e8539>.

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